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Adaptive responses and local stressor mitigation drive coral resilience in warmer, more acidic oceans

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Coral reefs have great biological and socioeconomic value, but are threatened by ocean acidification, climate change and local human impacts. The capacity for corals to adapt or acclimatize to novel environmental conditions is unknown but fundamental to projected reef futures. The coral reefs of Kāne'ohe Bay, Hawai'i were devastated by anthropogenic insults from the 1930s to 1970s. These reefs experience naturally reduced pH and elevated temperature relative to many other Hawaiian reefs which are not expected to face similar conditions for decades. Despite catastrophic loss in coral cover owing to human disturbance, these reefs recovered under low pH and high temperature within 20 years after sewage input was diverted. We compare the pH and temperature tolerances of three dominant Hawaiian coral species from within Kāne'ohe Bay to conspecifics from a nearby control site and show that corals from Kāne'ohe are far more resistant to acidification and warming. These results show that corals can have different pH and temperature tolerances among habitats and understanding the mechanisms by which coral cover rebounded within two decades under projected future ocean conditions will be critical to management. Together these results indicate that reducing human stressors offers hope for reef resilience and effective conservation over coming decades.

1. Introduction

Human impacts on coral reefs have resulted in the loss of roughly half of the world's live coral cover over the last 50 years [1–3]. Much of this decline has been driven by local impacts, such as sedimentation, coastal pollution and overfishing [4–6]. However, the downward trajectory of many reefs has accelerated over recent decades as coral bleaching (the loss of algal symbionts or algal pigments under stress) and associated coral mortality has increased because of climate change [7]. Projections of future ocean acidification and climate change have led many to conclude that coral reefs could collapse globally within the next few decades [8–10].

Seasonal maximum temperatures vary by about 10°C (24–34°C) across the geographical distribution of reefs, and coral thermal tolerances generally correspond to this regional temperature variation [11,12]. Corals tend to undergo bleaching at sustained temperatures greater than 1°C above the seasonal maximum to which they are accustomed, and often die when the bleaching is severe or prolonged. This regional variation in thermal tolerances shows that coral species clearly have the capacity to adapt to differing temperature regimes, but the rate of adaptation is unknown, and is generally believed to be too slow for corals to respond to the rapid climate change occurring today [8–10]. In addition, some corals experience a degree of acclimatization when exposed to higher temperatures [13], but the importance of such responses under climate change remains equivocal [14–16]. At least some individuals of some species are capable of surviving under reduced pH [17,18], but unlike temperature, the capacity for corals to adapt or acclimatize to ocean acidification remains almost completely unknown. Adaptation via natural selection,

physiological acclimatization, symbiont shuffling or other mechanisms may underlie changes in coral temperature and pH tolerances [11–15] and we refer to these processes collectively as adaptive responses. If corals are incapable of rapid, adaptive responses under global change, then the majority of reefs are projected to collapse once climate change reaches 1.2°C above the preindustrial [10], a value which will probably be exceeded within the next decade. Thus, given the assumptions underlying these predictions and recent global declines in coral cover, some argue that the collapse of coral reefs as we know them may already be inevitable [15,19,20].

In contrast to these dire predictions, others point to the persistence of reefs during past episodes of climate change, as well as the diversity of coral responses to warmer temperatures and ocean acidification [21–24]. Such studies caution that we ought to consider the possibility that corals could mount adaptive responses to global change over relevant timescales. Indeed, projections of reef futures which include modest increases in coral thermal tolerances often show widespread reef persistence under moderate global change scenarios, but still predict severe impacts under higher rates of acidification and warming [25,26]. Thus, our ability to predict probable future conditions depends on understanding the rate and capacity for adaptation. However, the fate of coral reef ecosystems will be determined by not only the adaptive responses of corals under anthropogenic stressors, but also by the resilience of these systems in a changing ocean. Resilience is defined here as the capacity to re-establish and maintain key ecological functions following disturbance [27,28]. Human impacts on reefs are causing increased coral mortality and may also work together to erode ecosystem resilience by increasing nutrients, reducing herbivory, slowing coral growth rates and inhibiting coral recruitment, thereby reducing the scope of these systems to recover after disturbance [5,29–31]. Better understanding the capacity for corals to respond to global change and the resilience of reef ecosystems under anthropogenic stressors is therefore critical for predicting reef futures.

Kāneʻohe Bay, Hawaiʻi provides a classic example of the devastating effects that human impacts can have on a coral reef system. Prior to Western contact, an extensive system of combined agriculture and aquaculture in Kāneʻohe supported a human population larger than the present-day one for over 750 years without detectable declines in reef condition [6]. From the 1930s to the late 1970s, however, the combined effects of urbanization, dredging, coastal development and sewage discharge into the bay caused severe impacts, notably the catastrophic loss of live coral cover. Bay-wide, coral cover on shallow reefs (0–2 m depth) was reduced by an average of greater than 70% by the early 1970s, and by greater than 95% in the southern sector of the bay, nearest the sewage input. After the sewage outfalls were relocated in 1977–1978, coral cover in the bay increased rapidly, returning to pre-eutrophication levels (50–90% coral cover) within 20 years [6,32,33]. Growth of remnant colonies as well as the recruitment of new individuals via larval settlement both appears to have contributed to this re-establishment of corals. In the southern sector of the bay, where corals were nearly extirpated during the time when sewage effluent flowed directly into the bay, recruitment appears to have been the dominant mechanism facilitating coral recovery [34]. Coral community structure

is not well characterized prior to the onset of the sewage input, and it is possible that the community composition today differs from the historical one. At present, coral communities are essentially indistinguishable in the severely impacted south bay as compared to the minimally impacted north bay, indicating that any changes in coral community structure were either subtle or very wide-reaching. During this 20-year recovery phase and subsequently, the reefs have experienced a variety of anthropogenic impacts including the introduction of invasive macroalgae species, freshwater kills in 1987 and 2014 (exacerbated by stream channelization), coral bleaching events in 1996, 2004, 2014 and 2015, coral disease outbreaks in 2011, 2012 and 2015 (possibly exacerbated by human stressors), periodic sewage spills, as well as chronic, moderate levels of urban runoff, sedimentation and fishing pressure [6,33,35]. In spite of these ongoing stressors, coral cover remains at 50–90% on most reefs throughout Kāneʻohe Bay, among the highest reported for any reefs in the Hawaiian Islands [4,36]. Despite numerous events that dramatically reduced live coral cover over recorded history, the coral reefs of Kāneʻohe Bay have shown surprisingly high levels of resilience over decadal timescales in the face of considerable human stressors.

The rapid recovery of coral reefs in Kāneʻohe Bay is even more remarkable, because it occurred under low pH and high temperature as compared to typical conditions for the region. Calcification and net heterotrophy within Kāneʻohe Bay reduce seawater pH by 0.1–0.2 units (mean pH approx. 7.85–7.95) as compared to the open ocean or on many other Hawaiian reefs (mean pH approx. 8.05) [37–41]. Likewise, owing to shallow water depth and long residence time under summer heating, Kāneʻohe Bay also experiences elevated seawater temperatures which average 1–2°C higher than Hawaiian reefs more influenced by open ocean waters during the May–October warm season (mean monthly maximum temperature: 28.0°C in Kāneʻohe Bay; 26.4–27.0°C on many Hawaiian reefs; electronic supplementary material, figure S1) [12,41–43]. Beyond predictions based solely on CO₂ emissions, coastal seawater chemistry also depends on biological responses and future ecosystem feedbacks which make the area a valuable experimental system [44]. While no natural gradient today can accurately match future predicted environmental change, low-pH and high-temperature conditions similar to those in Kāneʻohe Bay are not expected to occur on many other Hawaiian reefs until at least the middle of the century under high CO₂ emissions, or the end of the century under moderate CO₂ emissions [25,45]. Many studies project that environmental conditions common in Kāneʻohe Bay are beyond the changes that corals can cope with over decadal timescales and will lead to the collapse of coral reefs later this century [8–10,45]. Contrary to such predictions, surprisingly, corals in Kāneʻohe Bay recovered from catastrophic human disturbance over a period of only approximately 20 years despite low pH and high temperature. This scenario allowed us a unique opportunity to examine the capacity for corals to adapt or acclimatize to warmer, more acidic conditions similar to those that many reefs are predicted to experience under future climate change and ocean acidification, and to explore the potential for adaptive responses that may underlie coral resilience to anthropogenic impacts.

2. Methods

(a) Collection sites and study species

For this study, individuals of three of the dominant Hawaiian coral species (*Montipora capitata*, *Pocillopora acuta* and *Porites compressa*) were collected from nearshore reefs adjacent to the Hawai'i Institute of Marine Biology (HIMB) in Kāne'ohe Bay (centred at 21°26'6" N, 157°47'12" W), and from nearshore reefs in Waimānalo Bay, 18 km to the southeast (centered at 21°19'36" N, 157°40'54" W). Reef water is exchanged with offshore waters more rapidly in Waimānalo Bay than in Kāne'ohe Bay, with a residence time in the order of hours rather than days to weeks [42,46]. As a consequence of the differences in residence time, seawater pH averages 0.1–0.2 units higher and seawater temperature averages 1°C lower in Waimānalo Bay than in Kāne'ohe Bay, closer to offshore conditions (electronic supplementary material, figure S1) [42,46]. These appear to be long-term environmental differences between the bays and provide a natural gradient in space that may approximate the one that many reefs are predicted to experience through time.

(b) Experimental approach

Nine branches from each of 10–12 widely distributed colonies per species were collected at both locations in October 2011 and returned to HIMB for experimentation. After collection, corals were given 2.5 months to acclimate to the same aquarium environment at HIMB, thereby excluding short-term history as a factor in their responses, before being evaluated for their pH and temperature tolerances in a three month, flow-through aquarium experiment. The study design consisted of exposing coral branches to one of three levels of mean pH (8.04, 7.88, 7.71 ± 0.02) and mean temperature ($+0^\circ\text{C}$, $+1.5^\circ\text{C}$, $+3^\circ\text{C} \pm 0.1^\circ\text{C}$, relative to present-day offshore) in a fully factorial design, resulting in nine environmental treatments with two replicate aquaria per treatment (18 aquariums total). These pH and temperature treatments bracket the range from average conditions on many Hawaiian reefs today to those expected at the end of the century under high CO₂ emissions. Seasonal maximum temperatures (26.7, 28.2, 29.7°C) were maintained for the first five weeks, after which temperatures were lowered by 1.5°C in all treatments (25.2, 26.7, 28.2°C) to mean annual temperatures (all temperature adjustments were made at a rate of 0.5°C d^{-1}), and corals were exposed to these conditions for an additional nine weeks. This treatment allowed us to examine the corals' fates following high-temperature stress. See the electronic supplementary material, figure S2 for a diagram of the experimental design.

(c) Response variables

After acclimatization (see the electronic supplementary material), the corals were randomly divided among the replicate aquaria with one nubbin per colony in each environmental treatment. Corals were assessed visually for bleaching (normal, pale or bleached), and survivorship (alive, less than 5% tissue loss; partial mortality, approx. 30–90% tissue loss; dead, no discernable live tissue) at the end of the experiment. Some corals which paled or bleached earlier in the experiment had already begun to recover pigment by the end, so we restrict our analysis to the survivorship data. Calcification rates were assessed via the buoyant weighing technique [47] and were normalized to both initial weight and to surface area. Surface area was estimated from photos of the nubbins using IMAGEJ [48], assuming that they were approximately circular in cross-section; those that died or experienced partial mortality were excluded from the calcification analysis.

(d) Statistical analyses

Survivorship data were analysed by Fisher's exact test, using raw, count data of the survivorship categories detailed above. Differences in survivorship were tested using *a priori* contrasts among the six groups of corals (3 species \times 2 collection locations), as well as among the three levels of temperature within each species, the three levels of pH within each species, and the three levels of pH within each species under high temperature only, to test for possible temp \times pH interactions, and a Bonferroni correction was applied to control for the familywise error rate. Calcification data were analysed by ANOVA for each method of normalization with temperature, pH, collection site and species as fixed factors and tank as a nested factor, followed by a Tukey HSD as a *post hoc*. Additional ANOVAs were fit individually for each species. Assumptions of normality and equality of variance for ANOVA were assessed via diagnostic plots of the residuals. All analyses were performed using the base functions in R v.3.5.2 [49]. Additional details regarding the methods are provided in the electronic supplementary material.

3. Results

(a) Environmental conditions

Available seawater temperature data for Kāne'ohe Bay, Waimānalo Bay and offshore waters are shown in the electronic supplementary material, figure S1, while chemistry data for these sites have been reported elsewhere [37–41,46]. Aquarium conditions during these experiments mimic diel variability observed on the reefs, but with different mean values to match the target experimental treatments described above as closely as possible (electronic supplementary material, figures S3 and S4; table S1). Time-series of pH in the aquariums are shown in the electronic supplementary material, figure S3.

(b) Bleaching, survivorship and calcification rates

As expected, the survivorship of corals exposed to higher temperatures was reduced compared to those in the present-day offshore temperature treatments (figure 1; electronic supplementary material, figure S5). By contrast, the impact of decreased pH on calcification was more variable, depending on temperature. Interestingly, at intermediate temperature and acidification calcification rates were as fast as or faster than those measured under present-day offshore conditions (figure 1; electronic supplementary material, figure S6).

Differences in thermal tolerance are shown most clearly by the survivorship data. Bleaching occurred only under elevated temperatures, and mortality was strongly associated with bleaching (figure 1; electronic supplementary material, figure S5). The six groups of corals (3 species \times 2 collection locations) fell into four statistically distinct groups based on their temperature tolerances (electronic supplementary material, table S2). From the most temperature-sensitive to most tolerant these were, *Poc. acuta* from Waimānalo Bay, *M. capitata* from Waimānalo Bay, *Poc. acuta* from Kāne'ohe Bay, and finally the group *M. capitata* from Kāne'ohe Bay and *Por. compressa* from both locations (figures 1 and 2). Hence, the two most temperature-sensitive species, *Poc. acuta* and *M. capitata*, showed significantly higher tolerances when originating from the high-temperature site, Kāne'ohe Bay, whereas the more temperature-tolerant species, *Por. compressa*, showed no difference in thermal tolerance between locations. Unlike temperature, pH had no significant effect on survivorship for

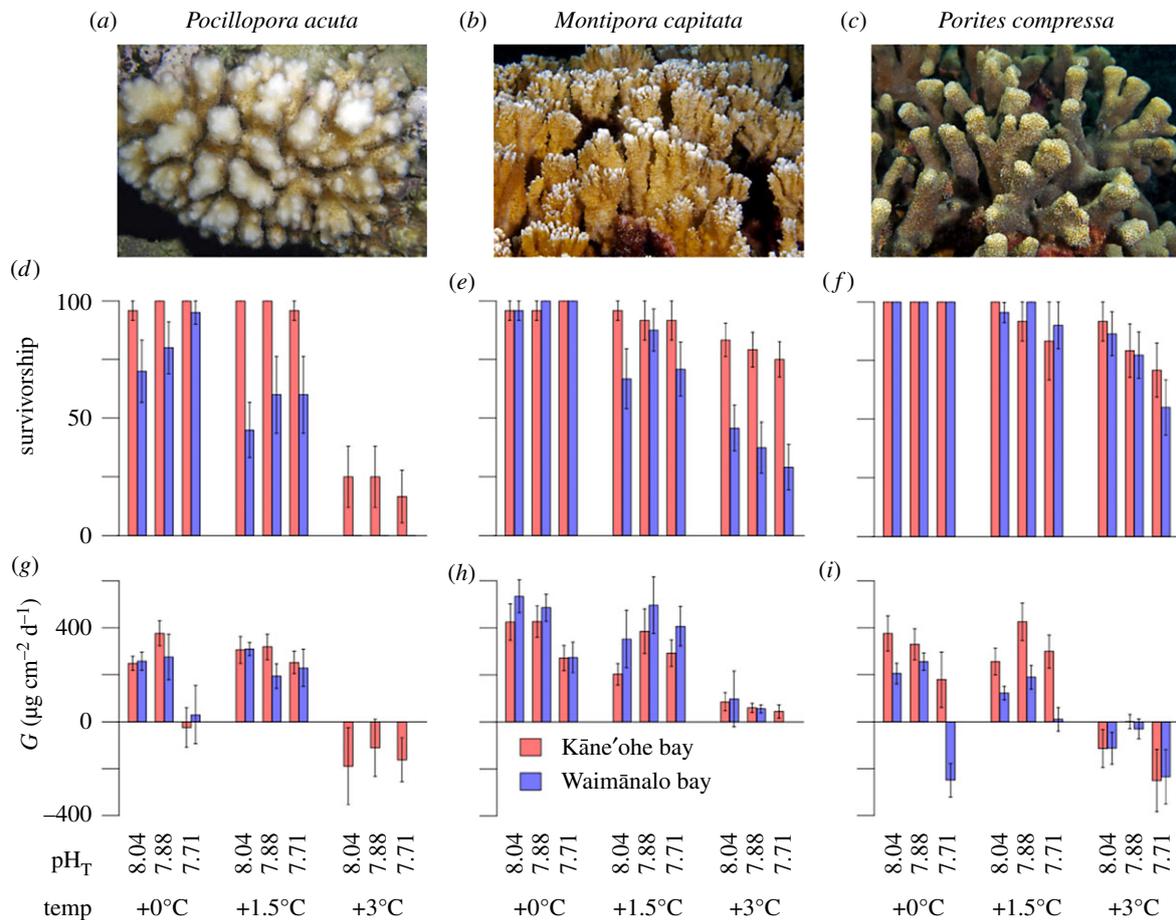


Figure 1. Effects of pH and temperature after three months of exposure on survivorship (*d–f*), and calcification rate (*g–i*) for the three coral species examined in this study (*a–c*), shown according to collection location. Seasonal maximum temperatures (26.7, 28.2, 29.7°C) were maintained for the first five weeks, after which temperatures were lowered by 1.5°C in all treatments (25.2, 26.7, 28.2°C) to mean annual temperatures, and corals were exposed to these conditions for an additional nine weeks. High-pH, low-temperature conditions occur at the Waimānalo Bay collection location, while the Kāne'ōhe Bay location experiences low-pH, high-temperature conditions. Where bars are not evident for *Poc. acuta* from Waimānalo Bay in (*d*), it is because all individuals in those treatments died (survivorship = 0). Sample size for survivorship data, $n = 10–12$ for most treatments (see the electronic supplementary material, figure S5). Corals which experienced partial mortality or died were excluded from the calcification analysis; data shown for treatments with $n = 2–12$ survivors. All data reported as mean \pm s.e.m. Photos courtesy of Keoki and Yuko Stender. (Online version in colour.)

any of the coral species, nor was there evidence of a significant pH \times temperature interaction on survivorship (figure 1; electronic supplementary material, table S2).

In contrast with the temperature tolerances, *Por. compressa* was the most pH-sensitive species, and it showed greater tolerance to acidification when originating from the low-pH site, Kāne'ōhe Bay (figures 1 and 2; electronic supplementary material, tables S3–S6). Conversely, *Poc. acuta* and *M. capitata* were more tolerant of acidification than *Por. compressa* from Waimānalo and showed no differences in pH tolerance between sites. Regardless of data normalization, the *Por. compressa* from Kāne'ōhe Bay calcified at significantly higher rates than those from Waimānalo Bay, whereas *Poc. acuta* and *M. capitata* from both locations calcified at statistically similar rates to conspecifics (figures 1 and 2; electronic supplementary material, tables S3–S6). Results of separate ANOVA fits for each species were very similar to these overall results and are reported in the electronic supplementary material, tables S7–S14. A portion (approx. 20%) of the calcification data have previously been reported in [50].

(c) Relative environmental tolerances

Relative coral temperature and pH tolerance distributions (figure 2) were estimated by changes in coral survivorship

and calcification rates under projected, future conditions, relative to present-day conditions. For the relative temperature tolerance calculation, the mean tolerance for each distribution was calculated as the proportional change in coral survivorship scores averaged across all the elevated temperature treatments (+1.5°C and +3°C for each level of pH), and relative to the maximum possible survivorship score (=100). The spread of each distribution was estimated from the standard deviation of the survivorship scores as a proportion of the maximum survivorship score, averaged across the same treatments. Relative pH tolerances were calculated in a similar way. The mean pH tolerances for each distribution was calculated as the proportional change in coral calcification rate averaged across the reduced pH treatments (7.88 and 7.71), relative to the overall mean calcification rate measured under the control pH treatment (8.04), but only for the low (+0°C) and intermediate (+1.5°C) temperature treatments, owing to low survivorship under the highest temperature treatments. The spread of each distribution was estimated from the standard deviation of the calcification rates as a proportion of the overall mean calcification rate under the control pH (8.04). It is interesting to note that species vary either their temperature or pH tolerance, depending on their intrinsic susceptibilities, but none of the

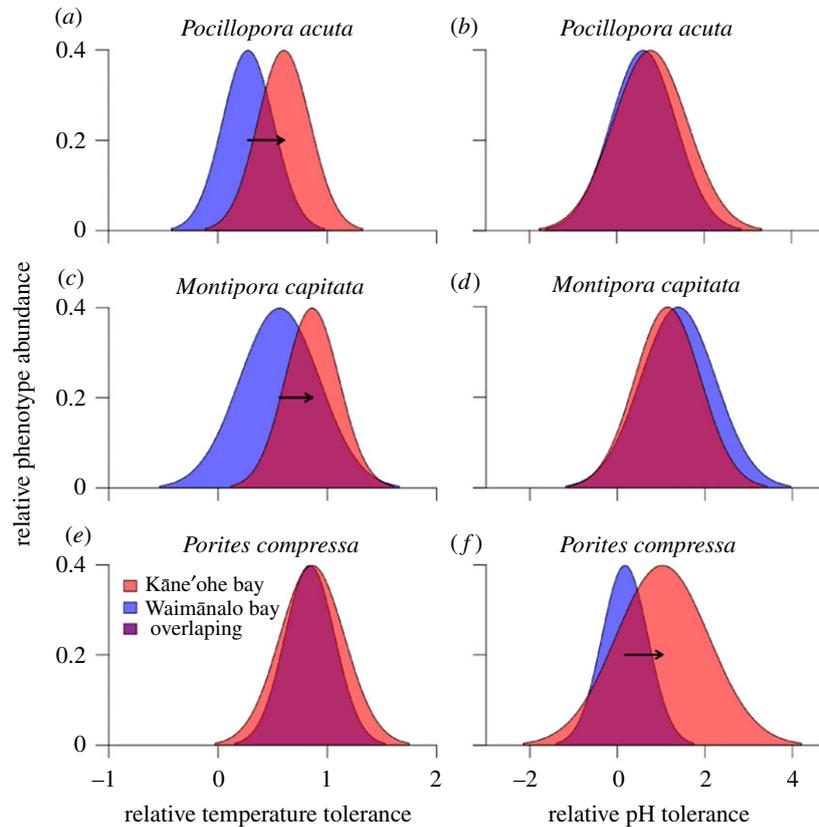


Figure 2. Reaction norms under elevated temperature (*a,c,e*) and reduced pH (*b,d,f*) for each coral species and collection location. Temperature tolerance distributions were estimated from changes in survivorship under elevated temperature, while pH tolerance distributions were estimated from changes in calcification under reduced pH, based on data shown in figure 1. Arrows indicate significant differences in tolerance among conspecifics between the two collection locations. (Online version in colour.)

species we tested show variable reaction norms between locations in response to both parameters (figure 2).

(d) Coral recovery and regrowth rates

Morphology of *Por. compressa* colonies are similar at the two collection locations, and they tend to form squat, hemispherical mounds of branches, but individuals from Kāneʻohe Bay average substantially higher calcification rates than those from Waimānalo Bay. Higher calcification could potentially lead to increased rates of linear extension and more rapid recovery of coral cover. To assess this possibility, colony morphology was measured for corals in the field ($n = 20$). Then, assuming that colony growth form corresponds to elliptical hemispheres, relative differences in skeletal density were estimated based on measured weight and surface area for the nubbins in this experiment and these data were combined with measured calcification rates to estimate relative differences in horizontal extension rates. Colonies in the field ranged in size from 0.3 to 1.5 m in diameter and showed a semi-major:semi-minor axis ratio of 1.76 ± 0.15 (mean \pm s.e.m.). Assuming similar branch morphology, skeletal density was significantly lower (one-way ANOVA; $F = 33.14$, $p < 0.001$) for corals from Kāneʻohe Bay than Waimānalo Bay by $16 \pm 2\%$. Under the intermediate temperature, intermediate pH treatment (which most closely approximates conditions in Kāneʻohe Bay) the corals from Kāneʻohe calcified 2.25 ± 0.15 times as fast as those from Waimānalo. Hence, three-dimensional rates of linear extension would be 2.67 ± 0.08 times higher in Kāneʻohe Bay for corals originating from Kāneʻohe than ones originating from Waimānalo.

Given the measured colony morphology and assuming growth occurs within an elliptical hemisphere, these linear extension rates would result in horizontal extension rates 2.13 ± 0.06 times faster for corals originating from Kāneʻohe. Hence, we estimate that the recovery of coral cover in Kāneʻohe Bay would have taken approximately 43 years if the corals experienced growth rates similar to the ones from Waimānalo, rather than the 20 year recovery time observed. This calculation assumes that losses in coral cover owing to disturbance would be equal when integrated over each recovery period, therefore, it may somewhat underestimate or overestimate the necessary timescale if corals from the two bays show markedly different susceptibilities to disturbance. Given these assumptions about horizontal extension rates, even the higher growth of corals from Kāneʻohe Bay would be insufficient to recover from greater than 95% decrease in coral cover within 20 years without considerable recruitment. Rather, this rapid increase in coral cover was driven by high calcification rates among corals which recruited after the sewage diversion, not simply the regrowth of a handful of particularly robust colonies that have survived and proliferated.

4. Discussion

Energetics and evolutionary theory argue that there ought to be trade-offs between physiological resistance and performance [51]. That is, increased tolerance to one factor is likely to come at the expense of reduced performance in some other aspect of physiology for an organism. It is interesting to note that the corals from Waimānalo Bay show contrasting hierarchies of temperature and pH tolerance: *Por. compressa*

are more tolerant to elevated temperature than *Poc. acuta* or *M. capitata*, but the latter two species are more tolerant to acidification than *Por. compressa* (figure 2). Given these results, one might hypothesize that these data point to physiological trade-offs between pH and temperature tolerances, and that corals are unable to achieve resistance to both factors simultaneously. The responses of corals from Kāneʻohe Bay show that this hypothesis is incorrect. The two most temperature-sensitive species, *Poc. acuta* and *M. capitata*, show increased temperature tolerances under the warmer conditions in Kāneʻohe Bay, yet maintain their high pH tolerances, and vice versa for the most pH-sensitive species, *Por. compressa*. Hence, at least some corals can achieve tolerance to both low pH and high temperature at the same time, but perhaps at the expense of other trade-offs that are not considered here.

Enhanced thermal tolerance gained by harbouring more resistant algal symbionts is associated with reduced growth rates in some corals [52,53], but we saw no evidence that such a trade-off is operating among these species. Although we did not identify the symbionts of our corals, Hawaiian *Poc. acuta* and *Por. compressa* are only known to associate with their preferred algal symbionts (C1d and C15, respectively) [54–56], suggesting a primary role of the coral host in determining the thermal limits for these species. By contrast, *M. capitata* hosts both thermally sensitive C31 symbionts as well as thermally tolerant D1a [54,57–59]. Host genotype and symbiont type each appear to contribute to variation in thermal tolerance among colonies of *M. capitata*, but even at our high-temperature, Kāneʻohe Bay site, approximately 80% of colonies are dominated by clade C [57–59]. Unlike some corals, increased thermal tolerance does not appear to result in significant reductions in growth for either *Poc. acuta* or *M. capitata* in our study system, and in fact, increased pH tolerance is associated with significantly higher growth rates among *Por. compressa*. Previous work has found that some coral species are more resistant to acidification than others [17,18], but our data show that pH tolerance also varies among individuals within a single population. Higher acidification tolerance is explained at least in part by differing pH upregulation, with the more resistant corals maintaining higher pH in their calcifying fluid and growing faster than sensitive individuals [50]. Regardless of the mechanisms, one possible explanation for this pattern is that the pH and temperature optima among these coral communities are shifted higher or lower at each site. If that is the case, then the heat-tolerant corals from Kāneʻohe should experience reduced performance under low temperatures, relative to those from Waimānalo, and likewise for the acidification-tolerant corals under high pH. Similar shifts in thermal optima have been shown for a coral across the Great Barrier Reef, where differences in performance manifest primarily at high- and low-temperature extremes [60]. While no obvious trade-offs to increased pH and temperature tolerance emerged during the three month timeframe of this study, trade-offs most likely exist; otherwise, these phenotypes should have already gone to fixation within the populations. If trade-offs exist between, for example, temperature and pH performance and disease susceptibility, we would not be able to see the effect until an outbreak strikes the population.

Several factors undoubtedly contributed to reef resilience in Kāneʻohe Bay, but both the diversion of the sewage outfalls

and the different pH and temperature tolerances among individual corals clearly played key roles in driving this recovery. Had the sewage input continued, the reefs almost certainly would have remained highly degraded. However, without individual variation from which to draw upon, it is very unlikely that the corals would have been able to colonize Kāneʻohe Bay in the first place, much less recover rapidly or persist under the naturally warmer, more acidic conditions found there. If corals around Oʻahu consistently showed temperature tolerances similar to the ones from Waimānalo Bay, with bleaching beginning to occur among the most sensitive taxa at 1°C above the offshore mean monthly maximum, then *Poc. acuta* and *M. capitata* would be expected to have undergone nearly annual bleaching in Kāneʻohe Bay over the last 20 years, and to have suffered mass mortality events at least four times during that interval—conditions projected to induce reef collapse [10]. Instead of four mass mortality events, the corals in Kāneʻohe Bay experienced only four bleaching events over the last 20 years and those events were associated with relatively low rates of mortality (less than 10%) [12,61]. Increased thermal tolerance appears to be a prerequisite for individuals of these species to colonize Kāneʻohe Bay, or other high-temperature habitats, and to sustain themselves long-term [62]. A recent study finds that these responses have occurred within less than 50 years, rather than millennia [62]. Individual variation in thermal tolerances present within species provides the fodder needed for this colonization, and probably facilitated the recovery of these corals in Kāneʻohe Bay following catastrophic disturbance. Similarly, *Por. compressa* returned to pre-eutrophication levels of abundance in Kāneʻohe Bay within 20 years following the sewage diversion, but this recovery would have taken more than twice as long if colonies showed growth rates equal to those of conspecifics from Waimānalo Bay. Thus, increased temperature or pH tolerance relative to conspecifics from Waimānalo was a critical factor driving reef recovery in Kāneʻohe Bay for each of these species. Previous studies have underscored the importance of effective local management for maintaining reef resilience [5,28], but most studies have assumed that local coral populations do not harbour sufficient individual variation to be able to respond effectively to rapid global change [8–10]. We show that assumption is incorrect for at least these corals, which show adaptive responses to warmer, more acidic conditions as compared to adjacent communities, and the recruitment and growth of these more tolerant individuals accounts for the rapid increase in coral cover from among the lowest to among the highest in the archipelago within roughly 20 years [6,33]. Whatever mechanisms drive these community differences in temperature and pH tolerance, such responses are a key to maintaining future reef resilience.

The question now becomes, what mechanisms allow corals in these locations to show increased temperature and pH tolerance? Although our experiments in Kāneʻohe Bay seem to rule out short-term acclimatization, the mechanism remains unknown. Is increased resistance a function of long-term acclimatization? Is it simply that individuals which cannot handle these conditions are unable to survive and only the hardy members of the population are able to colonize Kāneʻohe Bay? Are these differences heritable and subject to selection? Ultimately, do the results presented here imply that whatever adaptive mechanism allowed corals to repopulate the warmer, more acidic water of

Kāneʻohe Bay will be widespread and fast enough to preserve the function of at least some coral reefs?

5. Conclusion

This study supports previous observations that some coral populations harbour individuals which can thrive in moderately warmer, more acidic conditions, and shows that in Hawaiʻi these corals were capable of rapidly (approx. 20 years) recolonizing damaged reefs even under continued anthropogenic stressors. Ocean acidification, climate change and local human impacts have all been implicated in the well-documented decline of coral reefs around the world [5,8]. The question facing society is not whether all human impacts to coral reefs can be avoided, but rather, can global and local stressors be reduced sufficiently to preserve the function of at least some reefs? While some studies have concluded that almost all coral reefs will be severely degraded over the next few decades, even under optimistic mitigation scenarios [8–10], such studies assume that corals will not be able to respond on relevant time scales. By contrast, the data we present here show that such projections probably underestimate the potential for corals and coral reefs to tolerate moderate levels of global and local human stressors, particularly given the synergy between moderate levels of acidification and warming. Further, models show that even modest acclimatization or adaptation can alter future predictions considerably [6,26]. This and other recent studies [50,62] demonstrate that at least some reef-building corals can mount adaptive responses to both ocean acidification and climate change, and such responses are key to the rapid recovery of coral cover in Kāneʻohe Bay following the removal of chronic eutrophication from sewage inputs. If coral populations elsewhere also harbour sufficient individual variation for temperature and pH tolerances as shown by those in Kāneʻohe Bay, then at least some may be capable of not

only persisting but continuing to thrive if climate change is limited to 2°C above preindustrial levels. Even under this ambitious mitigation scenario coral reefs will experience future bleaching events, especially during marine heatwaves, but some reefs may be able to recover from these disturbances if corals respond to the changing environment. Higher rates of acidification and warming or more intense local stressors will lead to progressively severe impacts on coral reefs, even on relatively resilient reefs like those in Kāneʻohe Bay, Hawaiʻi. Nonetheless, coral reefs are far from ‘zombie ecosystems, neither dead nor truly alive in any functional sense’ [63], and such statements are irresponsible because feasible pathways remain available to society to reduce anthropogenic stresses on coral reefs and achieve meaningful coral reef conservation over coming decades.

Data accessibility. Data are available from the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.c06p34h> [64]. Data from this manuscript are accessible through the Biological and Chemical Oceanography Data Management Office (BCO-DMO) of the U.S. National Science Foundation.

Authors' contributions. C.P.J. and R.J.T. designed the experiments, analysed the data and wrote the paper. C.P.J. conducted the experiments.

Competing interests. We have no competing interests.

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